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Supposed Triassic bryozoans in the Klipstein Collection from the Italian Dolomites redescribed as calcified demosponges

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Synopsis. Type and other specimens of supposed bryozoans described by Klipstein (1843–5) from the Triassic Cassian Formation (Carnian) of the Italian Dolomites are redescribed. All of Klipstein's figured specimens are shown to be calcified demosponges ('sclerosponges') and not bryozoans. *Ceriopora alpina* Klipstein is referred to *Leiospongia* d'Orbigny and a valid type species (*Achilleum verrucosum* Münster) is selected for this genus to replace a previous invalid selection. Probable spicules are identified in *L. alpina* and an un-named congeneric species. *Catenipora orbignyana* Klipstein and *Calamopora ? gnemidium* Klipstein are both assigned to the new genus *Cassianochaetetes*, the former as the type species. *Achilleum polymorphum* Klipstein is also revised and placed in *Leiospongia*. Non-type material in the Klipstein Collection includes further calcified demosponge specimens identified as *Leiospongia* sp., ?*Cassianochaetetes milleporatus* (Münster, 1841), *Cassianochaetetes* sp., and *Atrochaetetes lagaaiji* (Bizzarini & Braga, 1978). Whereas a high diversity of calcified demosponges is evident in the Cassian Formation, only one true bryozoan, identified as the trepostome *Dyscritella zardinii* Schäfer & Fois, has been recognized among Klipstein's material. It is probable that several other Triassic calcified demosponges have been misidentified as bryozoans, usually as cerioporine cyclostomes. Morphological criteria for distinguishing bryozoans from calcified demosponges are given.

INTRODUCTION

Knowledge of the 'sclerosponges' (a polyphyletic grouping of demosponges with a calcareous basal skeleton, henceforth referred to as 'calcified demosponges') from the Cassian Formation (Lowermost Carnian) of the Dolomites (northern Italy) is very poor in spite of their abundance as fossils. Several species have been misidentified in the past as bryozoans and their descriptions are therefore to be found in the bryozoan literature. Other problems arise from insufficiently detailed descriptions of species and misinterpretations of earlier works.

Most of the type material of Münster (1841) and the entire Klipstein Collection (Klipstein 1843–45) of 'calcified demosponges' from the Cassian Formation have never been restudied. Recently, one of us (PDT) rediscovered type material of Klipstein (1843–45) in the Bryozoa collection of the BM(NH). More of Klipstein's material was found subsequently in the sponge collection. Among these finds are four figured syntypes. The purpose of this paper is to redescribe these syntypes and additional associated material from the Klipstein Collection, and to establish the status of these species as calcified demosponges and not bryozoans. Opportunity is taken to outline some of the differences between Triassic calcified demosponges and the bryozoans with which they are frequently confused.

History of the Klipstein Collection in the British Museum (Natural History)

At the time of publication of his 'Beiträge zur geologischen Kenntnis der östlichen Alpen', August von Klipstein was a professor of geology at the University of Giessen (now in West Germany). In 1851 he sold his entire fossil collection (6147 specimens) from the Alps, which consisted mainly of fossils from the Cassian Formation (5362 specimens), for the then enormous sum of £250 to the British Museum (according to correspondence kept in the MS collections of the Department of Palaeontology Library). The significance of some of Klipstein's specimens as types seems not to have been appreciated following incorporation of the specimens into the BM(NH) collections, and the existence of these important specimens in the BM(NH) has been widely overlooked by palaeontologists. For example, Flügel (1963) reported that the type specimens of Klipstein's 'bryozoan' species were missing.

The Klipstein Collection of Triassic calcified demosponges

Klipstein (1843–45) described 19 new species of calcareous sponges (including supposed bryozoans) from the Cassian Formation of St Cassian (Italy). Figured specimens belonging to 16 of these species have been recognized in the collections of the BM(NH):

'Calamopora' gnemidium (S10464, S10466, S10467, each a different species)
'Catenipora' orbignyana (S10465)
'Ceriopora' alpina (S10463)
'Achilleum' poraceum (S9541)
'Achilleum' polymorphum (S9540)
'Manon' pertusum (S9550)
'Manon' poraceum (S9545)
'Tragos' acute-marginatus (S9544)
'Tragos' sulcatum (S9542)
'Tragos' spongiosum (S9543)
'Scyphia' hieroglypha (S9551)
'Scyphia' polymorpha (S9548 – pl.19, fig.12a only)
'Scyphia' ? armata (S9549 – pl.19, fig.13 only)
'Gnemidium' stellaris (S9546)
'Gnemidium' concinnum (S9547)

The holotypes/syntypes of four Klipstein species are probably lost. These are:
'Tragos' involutum (1 specimen)
'Tragos' ramosum (both specimens figured under this name)
'Catenipora' spongiosa (1 specimen)
'Gnemidium' pyriforme (1 specimen)

The sponge nature of *'Stromatopora' porosa* (90014) is very questionable.

Locality and Stratigraphy

Klipstein's specimens came from the Cassian Formation, near St Cassian (Dolomites, northern Italy) according to both his publication and the original handwritten labels which survive with some of the specimens. However, Klipstein did not mention any specific locality in the St Cassian area. Most likely, his specimens are from the classical fossil localities of the 'Stuores-Wiesen' or 'Seeland-Alpe' near St Cassian. The stratigraphical age of these sections in the Cassian Formation has been studied by Urlichs (1974), who regarded them as lowermost Carnian (*aon* Subzone and *aonoides* Subzone).

Methods of study, sponge morphology and measurements

Before sectioning, external morphology was studied and photographed. The uncoated specimens were examined and micrographs prepared using back-scattered electrons with an ISI 60A SEM (see Taylor 1986).

Thin sections were prepared from all the important specimens to show details of internal morphology which are essential in discriminating between species.

The St Cassian calcified demosponges described here range in external morphology from dome-shaped to columnar or pedunculate (mushroom-shaped). Internally, the sponge is constructed of a mass of tubes or calicles. These calicles open onto the upper surface (or theca) of the sponge as a series of polygonal apertures. During life the theca would have been enveloped by the soft living tissue of the sponge. A system of shallow, radiating grooves (astrorhizae) may be visible on well-preserved thecal surfaces. Skeletal walls exterior to the living tissue are relatively smooth and form an epitheca which occurs at the base of the sponge but can also extend upwards around the stalk of pedunculate sponges. Multiple epithecae may occur in sponges which have regenerated.

New calicles are added to the growing sponge either by fissipar or intraparietal budding. In fissipar budding the lumen of the parent calicle is continuous with that of the daughter calicle, whereas in intraparietal budding this is not so and the daughter calicle arises entirely from the splitting of a calicle wall. Calicles are usually crossed at intervals by tabulae. The microstructure of the calicle walls and tabulae is similar and is either spherulitic or elongate spherulitic. Both fabrics consist of aragonite fibres arranged radially in spheres, but elongate spherulitic fabrics have preferential development of fibres orientated in the growth direction of the sponge (see Wood 1987: text-fig. 2). In some sponges, portions of calicles at varying distances beneath the theca become back-filled by aragonite fibres which may partly or completely block the lumen of the calicle. Rarely, spicules are incorporated in the calicle walls; these can be distinguished from superficially similar microborings by their straightness.

Measurements of calicle diameter, wall thickness and spherule diameter were made from thin sections using an eyepiece graticule fitted to a petrographical microscope. Whenever possible, measurements of the former two parameters were made from sections cutting calicles transversely. The minimum internal diameter of calicles was measured because this is less affected by section obliquity and wall thickness than is maximum external diameter (centre of wall to centre of wall).

SYSTEMATIC DESCRIPTIONS

An attempt has been made to describe fully the important specimens in the Klipstein Collection, utilizing characters visible externally as well as internal characters and skeletal microstructure. Because the systematics of 'coralline' sponges, 'sclerosponges', 'stromatoporoid' and 'sphinctozoan' sponges is currently under review by several workers (e.g. Vacelet 1985, Wood 1987), the higher level classification employed below must be regarded as tentative.

Klipstein's calcified demosponge species are re-assigned as follows:
Achilleum polymorphum Klipstein = *Leiospongia polymorpha* (Klipstein)
Ceriopora alpina Klipstein = *Leiospongia alpina* (Klipstein)
Catenipora orbignyana Klipstein = *Cassianochaetetes orbignyanus* (Klipstein)
Calamopora ? gnemidium Klipstein = *Cassianochaetetes gnemidius* (Klipstein)

Phylum **PORIFERA**
Class **DEMOSPONGIAE** Sollas, 1875
? Subclass **TETRACTINOMORPHA** Levi, 1956
? Order **AXINELLIDA** Bergquist, 1978
Family **incertae sedis**

Genus ***LEIOSPONGIA*** d'Orbigny, 1849

[= *Achilleum* Münster, 1834 (partim) (non ? *Achilleum* Goldfuss, 1826; non *Achilleum* Oken, 1815); *Ceriopora* Goldfuss, 1826 (partim); *Leiofungia* Fromentel, 1859 (obj. syn.); *Hartmanina* Dieci, Russo & Russo, 1975 (obj. syn.)].

DIAGNOSIS. Hemispherical sponges with almost straight calicles which are divided at irregular intervals by tabulae. Calicle walls and tabulae consist of spherules of aragonite. Spicules (style, acanthostyle or fusiform) are occasionally

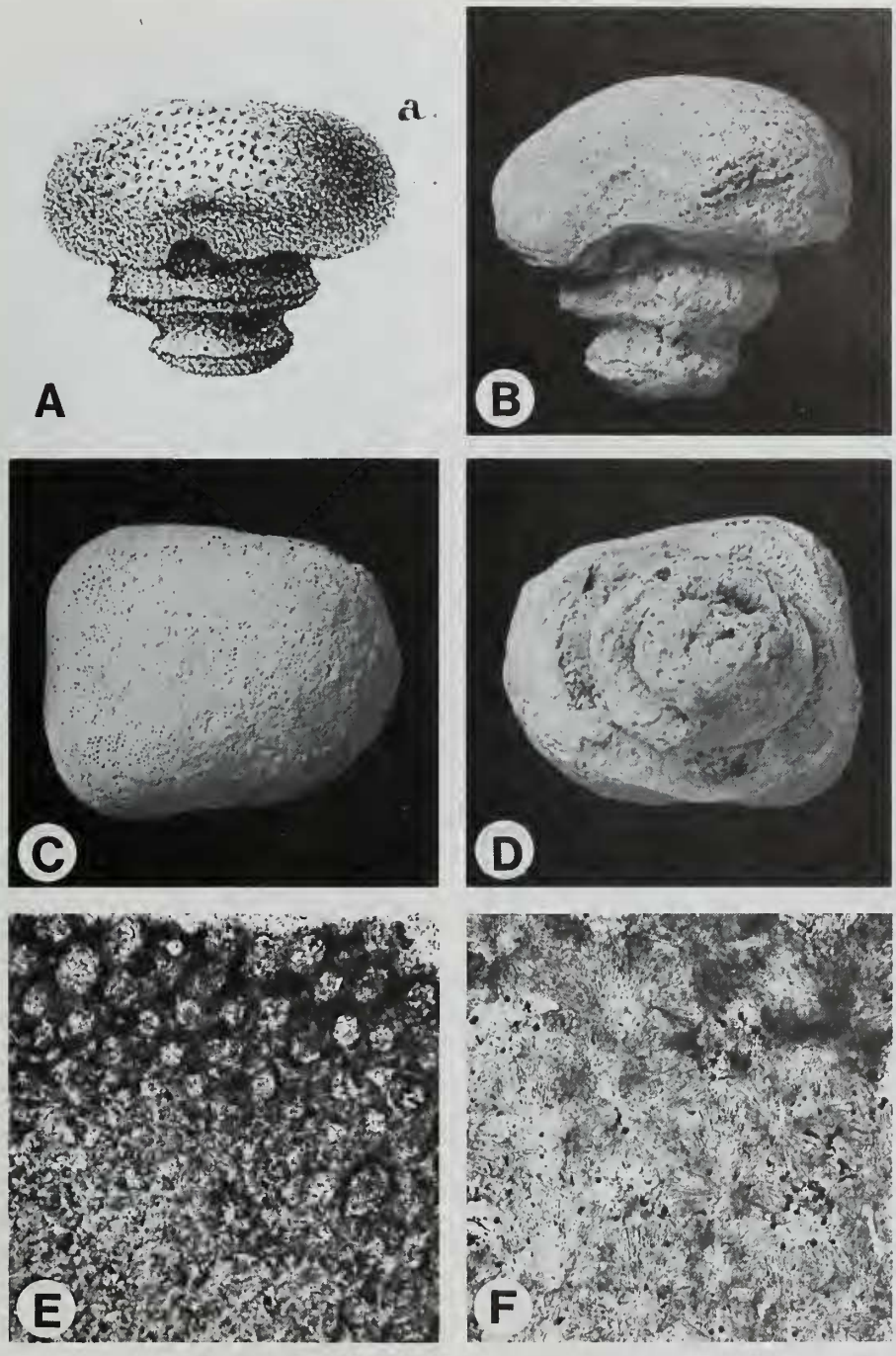

Fig. 1 *Leiospongia alpina* (Klipstein). Cassian Fm., St Cassian. Holotype, S10462. A, reproduction of pl.19, fig.17a of Klipstein (1845). B, side view, × 3·9. C, top view, × 3·9. D, underside showing epitheca, × 3·9. E, transverse sections of calicles, × 35. F, spherulitic wall structure, × 130.

incorporated into the walls and arranged parallel to growth direction. New calicles are added by fissipar division or intraparietal budding.

TYPE SPECIES. *Achilleum verrucosum* Münster, 1841, herein designated.

ATTRIBUTED SPECIES. *Leiospongia verrucosa* (Münster, 1841), *Leiospongia alpina* (Klipstein, 1845), *Leiospongia polymorpha* (Klipstein, 1845), '*Leiospongia*' sp.

REMARKS. The subsequent designation of '*Achilleum*' *milleporatum* Münster, 1841 as the type species of *Leiospongia* d'Orbigny, 1849 by de Laubenfels (1955: E100) is invalid and a new type species has to be chosen. This is necessary because

the *International Code of Zoological Nomenclature* stipulates that the type species of a genus has to be chosen from species included in the original description of the genus; *Achilleum milleporatum* is not among the species listed in the original description of *Leiospongia*.

The reason why de Laubenfels (1955) chose an inappropriate type species of *Leiospongia* apparently stems from the fact that Alcide d'Orbigny published his new genus in two publications which appeared almost simultaneously. These publications are: 'Note sur la classe de Amorphozoaires' (in *Revue et Magasin de Zoologie*, (2 ser.) **1**: 545–550); and *Prodrôme de paléontologie*, etc. (1: 240). The latter is the far better known publication, whereas the former is seldom cited. It is important to establish which was published first. The cover date of the relevant issue of *Revue et Magasin*, given as November, 1849, is quite probably incorrect as session reports from various societies up to 26 November 1849 are included in this issue of the journal. However, the *Revue et Magasin* was a monthly journal and the deadlines given for subscriptions in the January issue make it quite plausible that the journal was published during the month following that given on the cover. Furthermore, all catalogues that we consulted (e.g. Royal Society of London 1870, Neave 1939) give the publication date of the November issue as 1849. In the absence of contrary evidence, the date of publication of d'Orbigny's ' Note sur la classe de Amorphozoaires' is therefore interpreted as 31 December 1849, and we refer to it as d'Orbigny (1849).

The date of publication of d'Orbigny's *Prodrôme de paléontologie* etc., **1**, in which he attributed further species to *Leiospongia* including *Achilleum milleporatum* Münster, 1841, can be determined fairly precisely. D'Orbigny presented a copy of the work as a gift to the Société géologique de France during the session of the society on 21 January 1850 (see *Bull. Soc. géol. Fr.*, Paris, (2) 7: 98–99). Earlier sessions of this society had taken place on 4 January and 14 January but, although d'Orbigny attended these sessions, he did not present his work. Therefore, publication is likely to have been sometime between 14 and 21 January, and we interpret the year of publication as 1850.

Only species-group names included in d'Orbigny's first description (d'Orbigny 1849) of *Leiospongia* d'Orbigny, 1849 can qualify as potential type species. These are: *Achilleum verrucosum* Münster, 1841 and *Achilleum granulosum* Münster, 1841. Since the type specimen of *Achilleum granulosum* Münster, 1841 is still not redescribed, we herein designate *A. verrucosum* as the type species of the genus *Leiospongia* d'Orbigny, 1849. The holotype of this species has been redescribed by Dieci *et al.* (1975). Unaware of the above mentioned problems, they have chosen *A. verrucosum* Münster, 1841 as the type species of their new genus *Hartmanina*, which is, *ipso facto*, an objective junior synonym of *Leiospongia* d'Orbigny, 1849.

Leiofungia Fromentel, 1859 is an intended but unjustified emendation of *Leiospongia* d'Orbigny, 1849.

Zittel (1878) regarded *Leiospongia* as 'related to certain calcareous hydrozoans (*Millepora*)'.

Leiospongia alpina (Klipstein, 1845) Fig. 1

1845 *Ceriopora alpina* Klipstein: 286; pl. 19, figs 17a, b.
1963 *Ceriopora alpina* Klipstein; Flügel: 228.

DIAGNOSIS. The calicles are straight and are occasionally backfilled with aragonite. Possible monaxon megascleres may be embedded in the walls, orientated parallel to growth direction. Calicle diameter about 0·10 mm.

HOLOTYPE. BM(NH) S10462 (specimen and 1 thin section); figd Klipstein 1845: pl. 19, figs 17a, b. This is the only unequivocal syntype and is therefore taken to be the holotype. Fig. 1A–F.

OTHER MATERIAL. BM(NH) S10463 (specimen and 1 thin section), Klipstein Colln.

LOCALITY AND HORIZON. St Cassian, Italy, Cassian Formation, lowermost Carnian.

DESCRIPTION. The holotype shows a growth-form with multiple epithecae. The calicles are almost straight and are occluded at intervals by tabulae or an irregular backfill. The walls are formed of aragonite spherulites which are beginning to recrystallize in the holotype. Tabulae mostly consist of a single row of spherulites. Apparent spicules (visible in S10463) are occasionally embedded in the calicle walls and are simple monaxon megascleres, orientated roughly parallel to growth direction (suggesting that spicule embedment occurred by chance), about 0·002 mm thick and at least 0·08 mm long; no microscleres have been found.

MEASUREMENTS (in mm)		S10462	S10463
calicle diameter:	mean	0·10	0·10
	S.D.	0·019	0·016
	range	0·07–0·15	0·08–0·12
	N	20	10
wall thickness		0·04–0·07	0·05–0·09
spherulite diameter		0·06–0·12	0·06–0·12

REMARKS. There are some doubts about the attribution of this species to the genus *Leiospongia* d'Orbigny, 1849 because the type species of *Leiospongia*, *L. verrucosa* (Münster, 1841), was redescribed in insufficient detail by Dieci *et al.* (1975), who gave no details of the spicules, calicle diameter or tabulae.

Leiospongia polymorpha (Klipstein, 1845) Fig. 2

? 1841 *Achilleum radiciformis* Münster: 25; pl. 2, fig. 20.
1845 *Achilleum polymorphum* Klipstein: 281; pl. 19, fig. 3.
? 1975 *Hartmanina radiciformis* (Münster) Dieci *et al.*: 143; pl. 51, figs 7, 8; pl. 52, fig. 2.

DIAGNOSIS. *Leiospongia* with straight calicles, mean calicle diameter about 0·15 mm, and thick walls.

HOLOTYPE. BMNH S9540, specimen and 1 thin section, Klipstein Colln. Fig. 2A–C.

LOCALITY AND HORIZON. St Cassian, Italy; Cassian Formation, lowermost Carnian.

DESCRIPTION. The specimen is 35 mm high and has a maximum width of 11 mm. The base of a broken-off branch is present. There is no visible epitheca and the astrorhizal system is very faint. The calicles are comparatively straight and partitioned by rare tabulae. The calicle walls, formed of large aragonitic spherules, are irregular and incomplete. Recrystallization, however, has obliterated other diagnostic features (e.g. presence or absence of spicules).

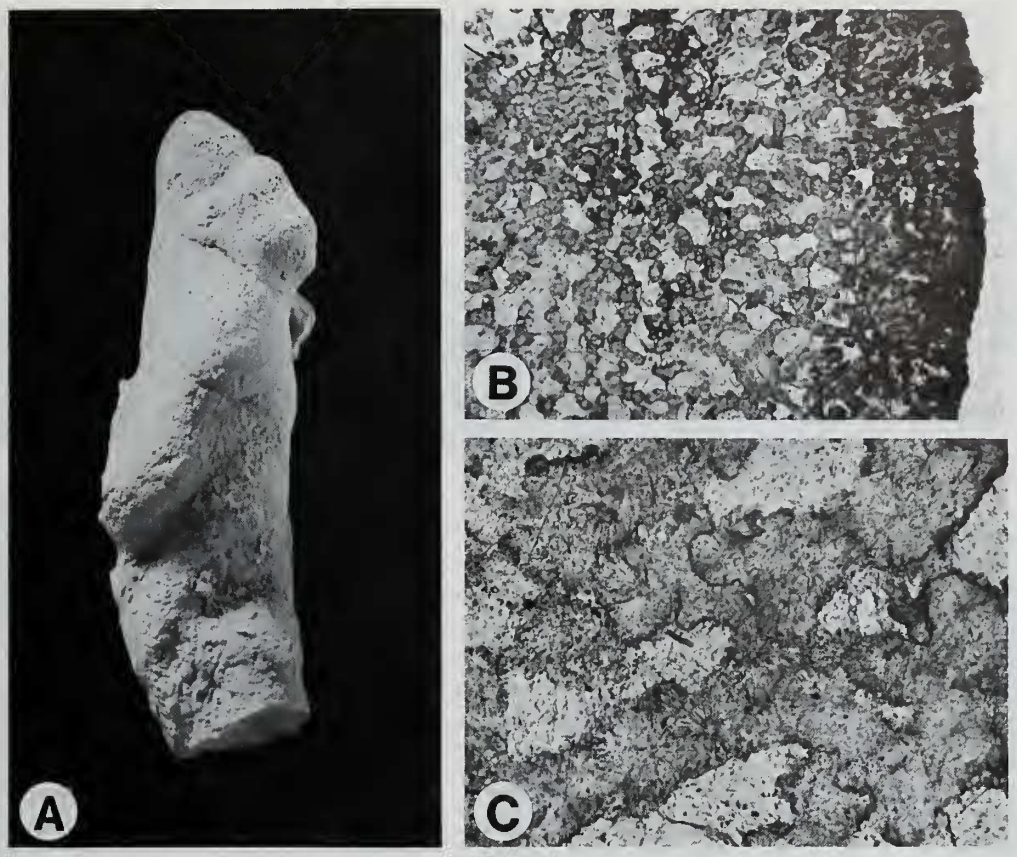

Fig. 2 *Leiospongia polymorpha* (Klipstein). Cassian Fm., St Cassian. Holotype, S9540. A, side view, × 2·5. B, transverse section, showing incomplete calicle walls, × 21. C, spherulitic wall structure, × 190.

MEASUREMENTS (in mm)	S9540
calicle diameter	0·09–0·20
wall thickness	0·04–0·15
spherulite diameter	0·05–0·15

REMARKS. The outer shape of *Leiospongia polymorpha* (Klipstein, 1845) resembles very much *'Hartmanina' radiciformis* (Münster, 1841) from the same locality. However, in their redescription of *'Hartmanina' radiciformis*, Dieci *et al.* (1975) give no details of such important diagnostic features as calicle diameter, tabulae shape, and wall thickness. Therefore, a more certain synonymy between *Leiospongia polymorpha* (Klipstein, 1845) and *'Hartmanina' radiciformis* (Münster, 1841) is impossible at the present time.

Leiospongia sp. Fig. 3

1845 *Calamopora* (?) *gnemidium* Klipstein: 285 (partim); pl. 19, fig.15b only (*non* pl. 19, figs 15a, 16a, b).

1963 *Ceriopora cnemidium* (Klipstein); Flügel: 228 (partim).

MATERIAL. BMNH S10464, Klipstein Colln. Fig. 3A–G.

LOCALITY AND HORIZON. St Cassian, Italy; Cassian Formation, lowermost Carnian.

DESCRIPTION. The sponge overgrows a coral fragment. Calicles are ill-defined; in the outer parts of the sponge they are divided by tabulae, whereas those in the basal parts are almost completely backfilled with aragonite. The tabulae consist of a single row of spherulites. Spicules, occasionally incorporated in calicle walls, are monaxon megascleres orientated parallel to growth direction, about 0·005 mm thick and up to 0·15 mm long.

MEASUREMENTS (in mm)	S10464
calicle diameter	0·12–0·18
wall thickness	0·06–0·10
spherulite diameter	0·04

REMARKS. This is the only calcified demosponge with an encrusting growth-form among the Klipstein material from St Cassian. The systematic value of the growth-form is unclear. The calicle measurements are slightly larger than those of *Leiospongia alpina* (Klipstein, 1845), and the spherulites of the basal skeleton are significantly smaller than those in both *Leiospongia alpina* and *L. polymorpha*. Therefore, there is some doubt about the assignment of this species to the genus *Leiospongia*.

Subclass **TETRACTINOMORPHA** Levi, 1956
Order **AXINELLIDA** Bergquist, 1978
Family **CERATOPORELLIDAE** Hartman & Goreau, 1972

Genus ***CASSIANOCHAETETES*** nov.

[= *Catenipora* Lamarck, 1816 (partim); *Ceriopora* Goldfuss, 1826 (partim); *Polytrema* Risso, 1826 (partim) (non *Polytrema*

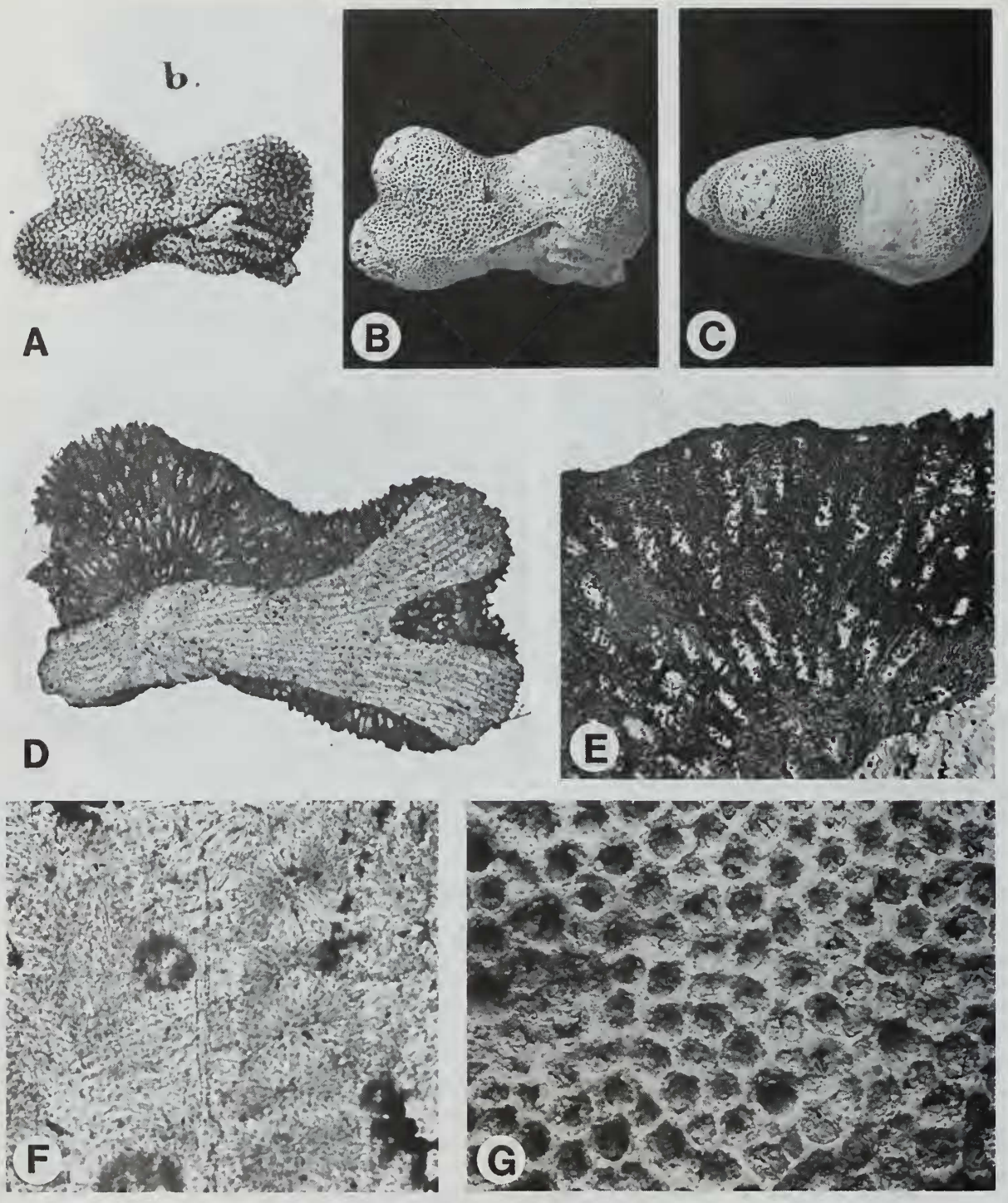

Fig. 3 *Leiospongia* sp. Cassian Fm., St Cassian. Specimen figured as *Calamopora* (?) *gnemidium* by Klipstein (1845: pl. 19, fig. 15b), S10464. A, reproduction of Klipstein's original figure. B, side view, × 4·2. C, top view, × 4·2. D, section showing dark-coloured *Leiospongia* sp. encrusting pale-coloured coral, × 7·6. E, oblique longitudinal section of calicles, × 21. F, spicule (centre) embedded in wall, × 375. G, scanning electron micrograph of thecal surface showing calicles, × 38.

Rafinesque, 1819); *Calamopora* Goldfuss, 1829 (partim); *Tragos* Münster, 1834 (partim) (non ? *Tragos* Goldfuss, 1826; non *Tragos* Schweigger, 1819); *Achilleum* Münster, 1834 (partim) (non ? *Achilleum* Goldfuss, 1826; non *Achilleum* Oken, 1815); *Leiospongia* d'Orbigny, 1849 (partim); *Actinospongia* d'Orbigny, 1849 (partim); *Leiofungia* Fromentel, 1859; *Actinofungia* Fromentel, 1859 (partim); *Leiospongia* de Laubenfels, 1955].

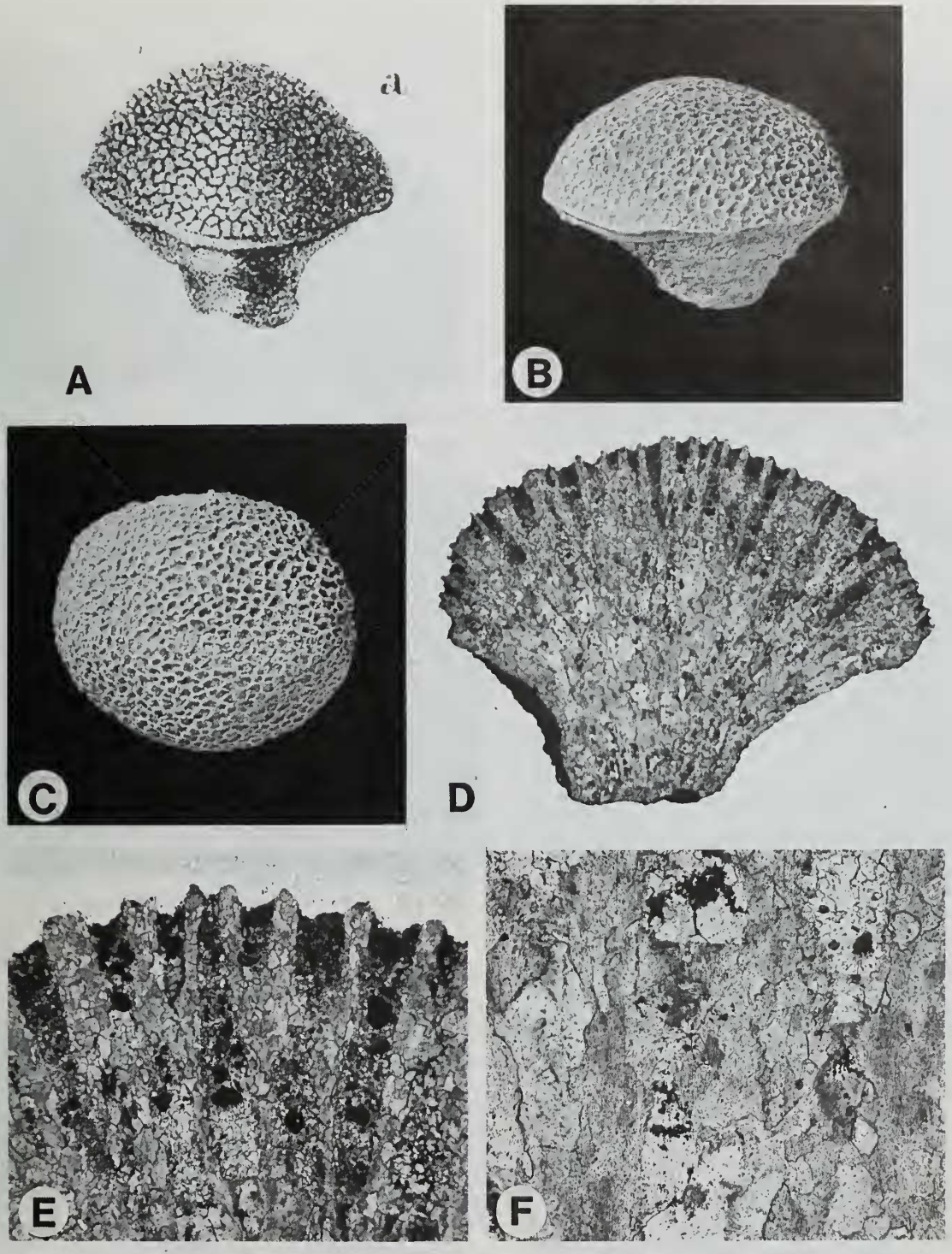

Fig. 4 *Cassianochaetetes orbignyanus* (Klipstein). Cassian Fm., St Cassian. Holotype, S10465. A, reproduction of pl. 19, fig. 20a of Klipstein (1845). B, side view showing basal epitheca, × 4·4. C, top view of thecal surface, × 4·4. D, longitudinal section, × 7·3. E, longitudinal section of calicles, × 20. F, tabulum with straight upper edge, × 55.

DIAGNOSIS. A ceratoporellid sponge with elongate spherulitic wall structure and tabulae in the calicles which consist of tufts of aragonite crystals. The horizontal elements may be developed as calicle narrowings, or as tabulae with a flat upper side and tufted lower surface, or as irregular calicle occlusions. The calicles are always bent. Incorporation of spicules into the skeleton has not been observed.

NAME. From the Cassian Formation. Masculine.

TYPE SPECIES. *Catenipora orbignyana* Klipstein, 1845.

REMARKS. *Cassianochaetetes* n. gen. differs from *Atrochaetetes* by the tabulae which have flat upper surfaces and tufted lower surfaces, and in the bent calicles. The Recent genus *Ceratoporella* differs in always having backfilled calicles.

The new genus *Cassianochaetetes* may be the same as *Leiospongia*, *sensu* de Laubenfels, 1955 and Dieci *et al.*, 1975 (non *Leiospongia* d'Orbigny, 1849). However, this opinion depends on the correct identification of a specimen from the Klipstein Collection as *Cassianochaetetes milleporatus* (see below, p. 48).

Species of this new genus have been previously assigned to ten different genera, all incorrectly. *Catenipora* Lamarck, 1816, *Ceriopora* Goldfuss, 1826 (revised by Nye, 1976) and *Polytrema* Risso, 1826 non Rafinesque, 1819 are all known or probable bryozoan genera. *Calamopora* Goldfuss, 1829 is a tabulate genus which has been suppressed by the plenary power of the ICZN (ICZN 1976). *Achilleum*, *sensu* Münster, 1834 and *Tragos*, *sensu* Münster, 1834 are not congeneric with the two available genera *Achilleum* Oken, 1815 and *Tragos* Schweigger, 1819, and are therefore inappropriate names for the sponges from St Cassian. *Actinospongia* d'Orbigny, 1849 (and *Actinofungia* Fromentel, 1859) is a calcareous sponge (Boule, 1923), while *Leiospongia* d'Orbigny, 1849 (and *Leiofungia* Fromentel, 1859) is a calcified demosponge with a conventional spherulitic wall structure (see above, p. 40).

ATTRIBUTED SPECIES. *Catenipora orbignyanus* Klipstein, 1845, *Calamopora* ? *gnemidium* Klipstein, 1845, *Achilleum milleporatum* Münster, 1841 and *Cassianochaetetes* sp. (p. 48), all from the Cassian Formation (lowermost Carnian) of the Italian Dolomites.

'Achilleum' reticulare Münster, 1841 and *'Achilleum' subcariosum* Münster, 1841, both from the St Cassian Formation of northern Italy, were attributed to *Leiospongia*, *sensu* de Laubenfels, 1955, by Dieci *et al.* (1975). However, they appear to be sufficiently different from *Cassianochaetetes* to justify separation at generic level. They are expressly excluded herein from *Leiospongia* d'Orbigny, 1849.

Cassianochaetetes orbignyanus (Klipstein, 1845) Fig. 4

	1845	*Catenipora orbignyana* Klipstein: 288; pl. 19, figs 20a, b.
	1850	*Leiospongia reticularis* d'Orb.; d'Orbigny: 209 (partim).
?	1865	*Leiofungia orbignyana* Klipstein; Laube: 243; pl. 2, fig. 15.
?	1911	*Leiospongia* cfr. *Orbignyiana* Klipstein sp.; Vinassa de Regny: 9.
?	1933	*Leiospongia* cfr. *orbignyana* Klipst.; Venzo, *in* Migliorini & Venzo: 148.
	1963	*Catenipora orbignyana* Klipstein; Flügel: 228.
?	1975	*Leiospongia orbignyana* (Klipstein); Dieci *et al.*: 139; pl. 51, fig. 2.

DIAGNOSIS. The calicles are slightly curved and large, about 0·4–0·5 mm in diameter. The epitheca shows well-developed growth lines.

HOLOTYPE. BMNH S10465 (specimen and 2 thin sections), figd Klipstein 1845: pl. 19, figs 20a, b. This is the only recognizable syntype and is therefore taken as the holotype. Fig. 4A–F.

LOCALITY AND HORIZON. St Cassian, Italy; Cassian Formation, lowermost Carnian.

DESCRIPTION. The sponge is fungiform with a convex theca, and is 9 mm high and 11 mm in maximum diameter. The epitheca is well-developed and displays growth lines. The calicles are strongly curved and are partitioned rarely by tabulae consisting of irregular tufts of aragonite crystals or by tabulae with flat upper sides and irregular tufts of aragonite crystals on their lower sides. There are no spicules incorporated in the walls. The wall structure consists of elongate spherules of aragonite crystals.

MEASUREMENTS (in mm)	S10465	
calicle diameter	*c.* 0·44	
wall thickness	0·09	(or greater)

REMARKS. D'Orbigny (1850: 209) regarded this species as a junior synonym of *'Achilleum' reticulare* Münster, 1841, an opinion not shared, however, by Dieci *et al.* (1975). Detailed re-examination of the holotype of *'Achilleum' reticulare* Münster, 1841 is required to settle the problem.

Most references to this species in the literature are doubtful (Laube 1865, Vinassa de Regny 1911, Venzo *in* Migliorini & Venzo 1933 and Dieci *et al.* 1975). However, confident reassignment of the specimens studied by these authors is precluded by the inadequacy of their descriptions and the small size of their figures.

Cassianochaetetes gnemidius (Klipstein, 1845) Fig. 5

	1845	*Calamopora ? Gnemidium* Klipstein: 285; pl. 19, fig. 15a (*non* pl. 19, figs 15b, 16a, b).
	1850	*Polytrema gnemidium* d'Orb.; d'Orbigny: 208.
?	1865	*Actinofungia astroites* Münster; Laube: 243 (*non* pl. 12, figs 6a, b).
	1878	*Calamopora Cnemidium* Kl.; Quenstedt: 548; pl.140, fig.46.
non	1889	*Ceriopora Cnemidium* Klipstein sp.; v. Woehrmann: 196, pl. 5, figs 21, 21a.
??	1911	*Ceriopora Gnemidium* (Klipstein); Vinassa de Regny: 16; pl. 2, fig. 12.
??	1936	*Ceriopora* cfr. *cnemidium* (Klipstein); Woehrmann; Kühn: 127.
	1963	*Ceriopora cnemidium* Klipstein; Flügel: 228.
non	1978	*'Ceriopora' gnemidium* (Klipstein, 1843); Bizzarini & Braga: 33; pl.1, figs 1–3.

LECTOTYPE. S10466 (specimen and 2 thin sections), figd Klipstein, 1845: pl. 19, fig. 15a. Each of Klipstein's three figured specimens of *Calamopora* ? *Gnemidium* is here regarded as a different species; selection herein of one of these figured specimens as the lectotype therefore leaves no remaining conspecific specimens which could be accorded the status of paralectotypes. Fig. 5A–F.

LOCALITY AND HORIZON. St Cassian, Italy; Cassian Formation, lowermost Carnian.

DESCRIPTION. Growth-form is semiglobular with a hidden epitheca, the incomplete sponge measuring over 35 mm in size. The astrorhizal system consists of very shallow furrows radiating from several dome-shaped mamelons. The calicles are bent and tabulae are rare and when present are formed of

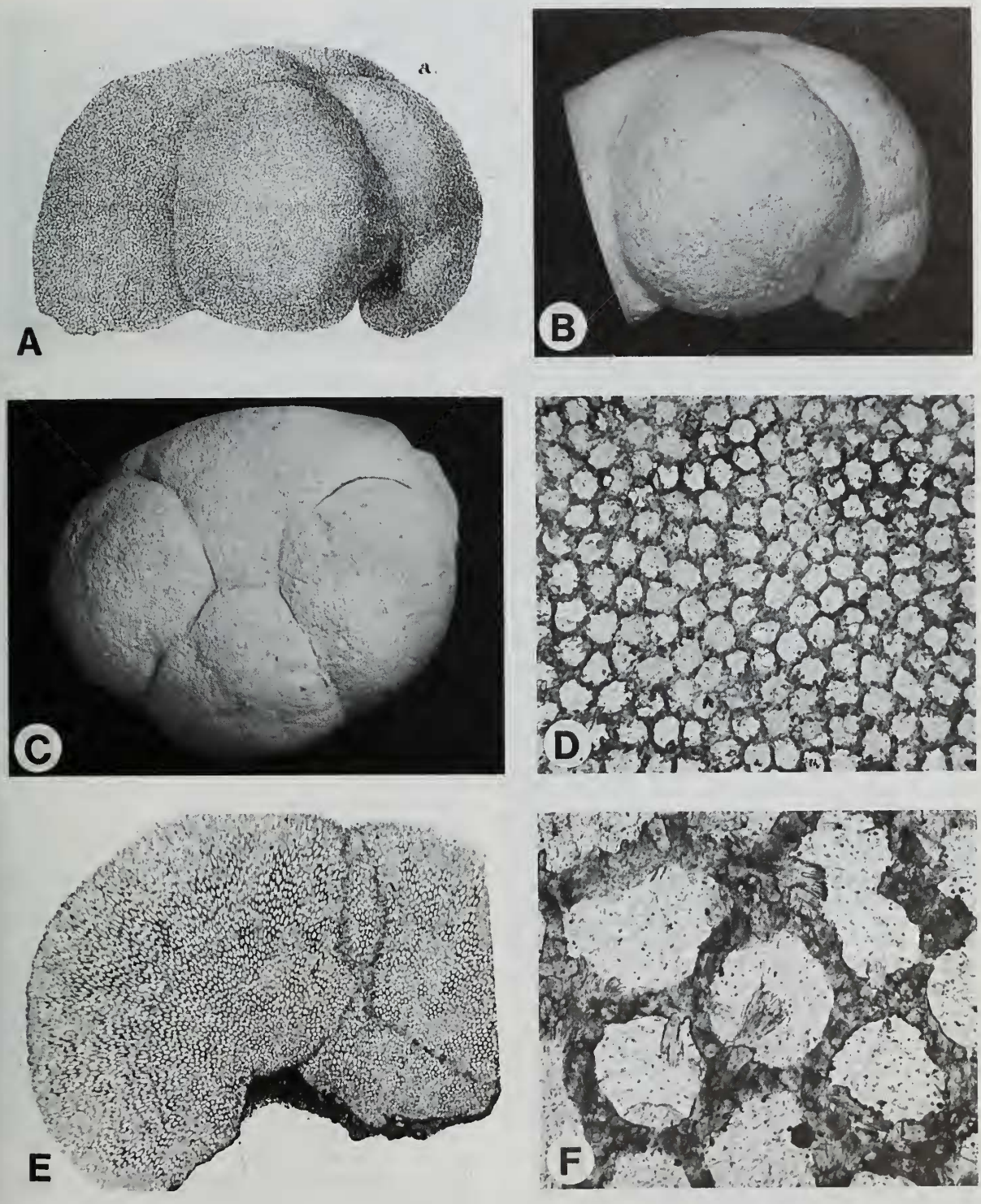

Fig. 5 *Cassianochaetetes gnemidius* (Klipstein). Cassian Fm., St Cassian. **Lectotype,** selected herein, S10466. A, reproduction of pl. 19, fig. 15a of Klipstein (1845). B, side view (bottom left corner of specimen has been cut off since Klipstein's figure was drawn), × 1·7. C, top view, × 1·6. D, transverse sections of calicles, × 21. E, section, × 2·9. F, tufts of aragonite crystals growing from calicle walls with elongate spherulitic microstructure, × 92.

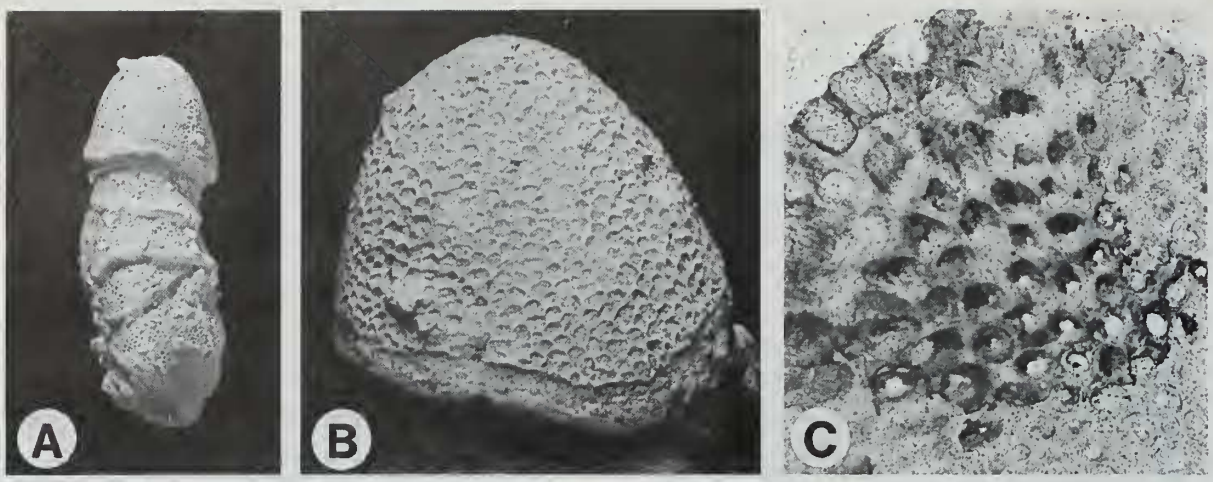

Fig. 6 ?*Cassianochaetetes milleporatus* (Münster). Cassian Fm., St Cassian. S10468. A, side view showing columnar form and multiple epithecae, × 3·8. B, scanning electron micrograph of thecal surface, × 16. C, section, × 32.

irregular tufts of aragonite crystals. Wall structure is elongate spherulitic. There are no spicules incorporated in the walls.

MEASUREMENTS (in mm)		S10466
calicle diameter:	mean	0·18
	S.D.	0·026
	range	0·12–0·24
	N	20
wall thickness		0·03–0·06

REMARKS. The species *'Calamopora' ? gnemidium* Klipstein, 1845 has very often been misinterpreted. This is partly because Klipstein (1845) figured under this name three different specimens, each a different species, and the species-group name *gnemidium* has never been restricted to any single one of these specimens. However, Woehrmann (1889) restricted *'Calamopora' gnemidium* to the two specimens figured by Klipstein (1845) as pl. 19, figs 15a and 15b (BMNH S10466 and S10464 respectively). Since the specimen figured on pl. 19, fig. 15b is a coral overgrown by a calcified demosponge (= *Leiospongia* sp., p. 43), the specimen figured on pl. 19, fig. 15a is here chosen as the lectotype of *'Calamopora' gnemidium* Klipstein, 1845.

Two different spellings of the species name appear in the literature, *gnemidium* and *cnemidium*. It is evident from Klipstein's paper that *gnemidium* is the original spelling; *cnemidium* is therefore an incorrect secondary spelling without nomenclatorial validity.

Most other references to this species cannot be verified because of the insufficiently detailed descriptions given. An exception is the reference to *'Ceriopora gnemidium'* in Bizzarini & Braga (1978) who described the species as showing '.. a structure made of granular calcitic laminae'. Their material certainly does not belong to *Cassianochaetetes gnemidius* (Klipstein).

? *Cassianochaetetes milleporatus* (Münster, 1841) Fig. 6

1841 *Achilleum milleporatum* Münster: 26; pl. 1, fig. 5.
1850 *Leiospongia milleporata* d'Orb.; d'Orbigny: 240.
1859 *Leiofungia milleporata*; Fromentel: 49.
1865 *Leiofungia milleporata* Münster; Laube: 241; pl. 2, fig. 12.
1878 *Achilleum milleporatum* Quenstedt: 541; pl. 140, figs 33–40, 48.
1879 *Leiospongia milleporata*; Zittel: 47.
1975 *Leiospongia milleporata* (Münster); Dieci *et al.*: 139; pl. 51, fig. 1; pl. 53, fig. 1.

MATERIAL. BMNH S10468 (specimen and 2 thin sections), Klipstein Colln. Fig. 6A–C.

LOCALITY AND HORIZON. St Cassian, Italy; Cassian Formation, lowermost Carnian.

DESCRIPTION. The specimen has a slender, columnar growth-form with multiple epithecae indicating regeneration. Each epitheca is short and the theca is strongly convex. The calicles appear to be curved. Tabulae and spicules have not been observed. The wall structure is elongate spherulitic, but the aragonite crystal bundles are strongly altered by the beginnings of sparitization.

MEASUREMENTS (in mm)	S10468
calicle diameter	0·10–0·15
wall thickness	*c.* 0·03

REMARKS. This description is included because *C. milleporatus* (Münster, 1841) is the type species of *Leiospongia* de Laubenfels, 1955 (non *Leiospongia* d'Orbigny, 1849). However, it is not absolutely certain that the specimen from the Klipstein Collection belongs to this species. The growth-form and the wall structure correspond with Münster's holotype, which has been redescribed by Dieci *et al.* (1975), but the dimensions and details of tabulae shape and calicle form have not been published.

Cassianochaetetes sp. Fig. 7

1845 *Calamopora ? gnemidium*; Klipstein: 285; pl. 19, figs 16a, b (*non* pl. 19, figs 15a, b).

MATERIAL. BMNH S10467 (specimen and 2 thin sections), figd Klipstein 1845: pl. 19, figs 16a, b. Fig. 7A–E.

LOCALITY AND HORIZON. St Cassian, Italy; Cassian Formation, lowermost Carnian.

DESCRIPTION. The specimen is fungiform, 8 mm high and has a maximum diameter of 9 mm. The epitheca is well-developed

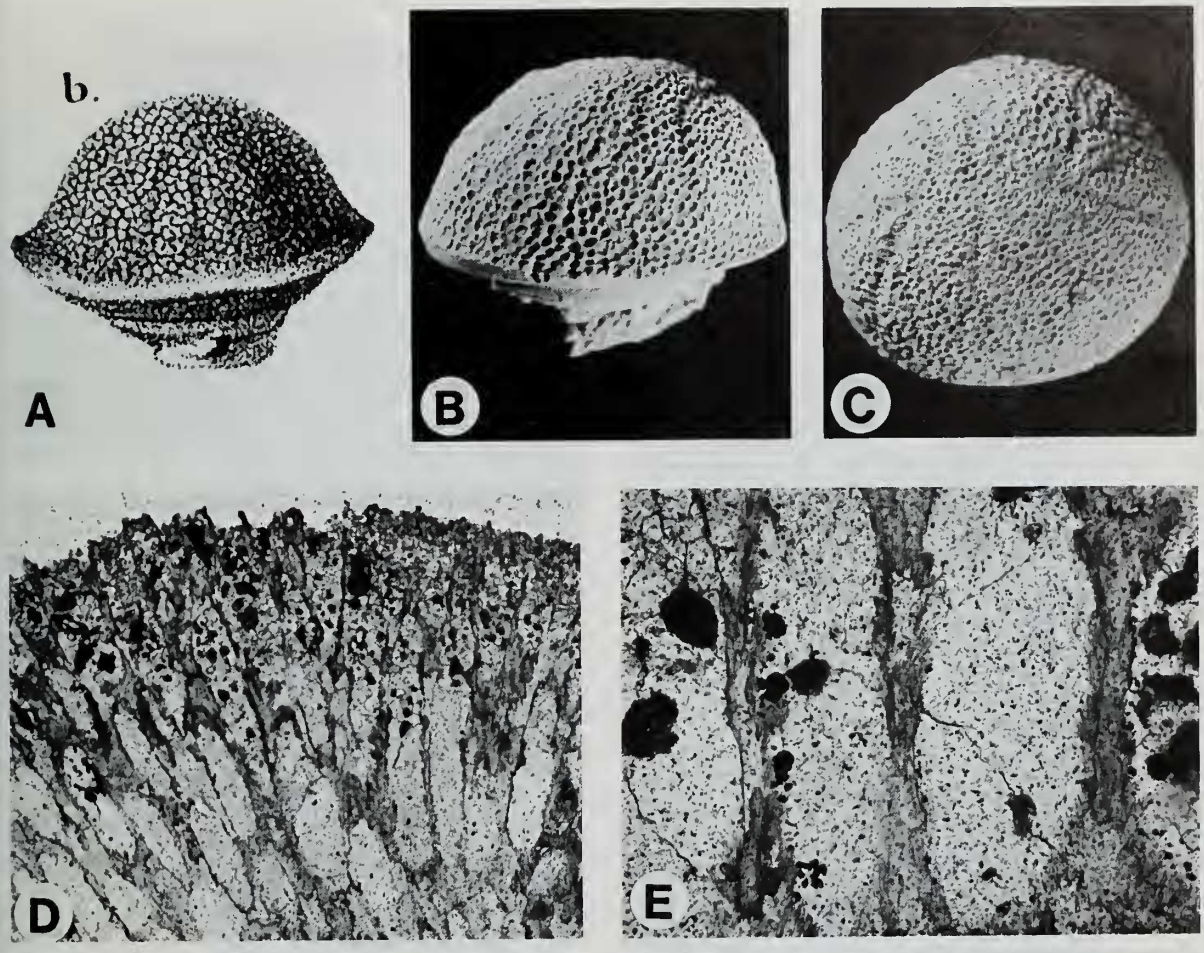

Fig. 7 *Cassianochaetetes* sp. Cassian Fm., St Cassian. Specimen figured as *Calamopora* (?) *gnemidium* by Klipstein (1845: pl. 19, figs 16a, b), S10467. A, reproduction of Klipstein's fig. 16b. B, side view, × 5·9. C, top view showing astrorhizae, × 5·9. D, oblique longitudinal section, × 21. E, calicle walls, × 89.

and shows growth lines. There is one astrorhizal system, radiating from the centre of the convex theca, consisting of shallow grooves which may bifurcate. The calicles are strongly bent and tabulae are very rare. Wall structure is elongate spherulitic. There are no spicules.

MEASUREMENTS (in mm)	S10467
calicle diameter	0·19–0·28
wall thickness	0·03–0·06

REMARKS. The general shape of the specimen most closely resembles *Cassianochaetetes orbignyanus*, but the calicles are much smaller, and the presence of an astrorhizal system is a further distinguishing feature. Although this probably represents a new species, it would be unwise to propose a new name on the basis of the single available specimen.

Some other Triassic calcified demosponges described as bryozoan genera

The bryozoan literature includes several other examples of Triassic fossils which are more likely to be calcified demosponges. For example, Schäfer & Fois (1987) list eight so-called cerioporine cyclostomes from the U. Triassic whose microstructures suggest that they may not be bryozoans. The Klipstein Collection contains material which permits a detailed description and reinterpretation of one such supposed bryozoan genus. In two other cases, we indicate possible synonymies and incorrect attributions. However, definite reassignments of many of these fossils must await detailed redescriptions of the type material.

1. *Seelandia* Bizzarini & Braga, 1978

Family **CERATOPORELLIDAE** Hartman & Goreau, 1972

Genus ***ATROCHAETETES*** Cuif & Fischer, 1974

[=*Seelandia* Bizzarini & Braga, 1978.]

REVISED DIAGNOSIS. Ceratoporellidae with horizontal elements in the tubes which consist of bundles of radiating crystals. The horizontal elements can be developed either as calicle constrictions, as tabulae with flat undersides, or as almost complete infillings of a segment of a calicle. New calicles arise by intraparietal budding (very common) or by fissipar division (very rare). An astrorhizal system may be present.

TYPE SPECIES. *Atrochaetetes tamnifer* Cuif & Fischer, 1974.

REMARKS. Bizzarini & Braga (1978) regarded *Seelandia* as a cyclostome bryozoan. However, *Seelandia* displays the same wall structure (elongate spherulitic, with no central wall axis) and tabulae shape (crystal bundles with straight undersides) as the 'chaetetid' *Atrochaetetes* Cuif & Fischer, 1974. Even though Bizzarini & Braga (1978) recognized these obvious similarities between *Seelandia* and *Atrochaetetes*, they were convinced of the bryozoan affinities of *Seelandia* and chose to propose a new genus rather than transfer the firmly-established 'chaetetid' *Atrochaetetes* to the Bryozoa. We regard *Seelandia* and *Atrochaetetes* as identical and therefore *Seelandia* Bizzarini & Braga, 1978 as a junior subjective synonym of *Atrochaetetes* Cuif & Fischer, 1974. The microstructure of the skeleton, its aragonitic composition (see below, p. 53), the shape of the tabulae, and the presence of an astrorhizal system in some species of *Atrochaetetes* such as *A. annoscai* (Bizzarini & Braga, 1978), indicate unequivocally that *Atrochaetetes* is a calcified demosponge.

Although well-preserved, our material of *Atrochaetetes* does not display any spicules. It is probable that the 'spicules' described by Dieci *et al.* (1977) in *Atrochaetetes 'medius'* Cuif & Fischer, 1974 [= *Atrochaetetes lagaaiji* (Bizzarini & Braga, 1978)] are borings made by thallophyte algae. Similar borings in our material may resemble spicules. By contrast, the spicules of *Meandripetra zardinii* Dieci, Russo, Russo & Marchi, 1977 are genuine; note the differences in general shape and size between the spicules of *Meandripetra* and the so-called 'spicules' of *Atrochaetetes* (Dieci *et al.* 1977: pl. 7, figs 3a–b; pl. 3, fig. 1).

ATTRIBUTED SPECIES. *Atrochaetetes tamnifer* Cuif & Fischer, 1974, *A. medius* Cuif & Fischer, 1974, and *A. alakirensis* Cuif & Fischer, 1974, all from the Carnian of Alakir Çay (Lycia, Turkey); *A. lagaaiji* (Bizzarini & Braga, 1978) and *A. annoscai* (Bizzarini & Braga, 1978), both species from the lowermost Carnian of the Cassian Formation; and *A. 'tamnifer'* Cuif & Fischer, 1974 of Cuffey *et al.* (1979), probably an undescribed species, from the Jurassic/Cretaceous Limestone near Orhaneli, northwestern Turkey.

Atrochaetetes lagaaiji (Bizzarini & Braga, 1978) Fig. 8

non 1974 *Atrochaetetes medius* n. sp.; Cuif & Fischer: 8; pl. 2, figs 2, 3.
1977 *Atrochaetetes medius* Cuif & Fischer; Dieci *et al.*: 236; pl.1, figs 6a, b; pl. 2, figs 4a, b; pl. 3, figs 3a–d.
1978 *Seelandia lagaaiji* n.sp.; Bizzarini & Braga: 40; pl. 5, figs 1–6.

MATERIAL. BMNH S10469 (specimen and 2 thin sections), Klipstein Colln. Fig. 8A–F.

LOCALITY AND HORIZON. St Cassian, Italy; Cassian Formation, lowermost Carnian.

DESCRIPTION. The specimen is 18 mm high and has a diameter of 12 mm. The epitheca is well developed and displays growth lines. The calicles are straight and intercepted by tabulae which have flat undersides and upward-pointing tufts of aragonite crystals on their upper sides. Tabulae are comparatively rare, there are large distances between successive tabulae in a calicle, their thickness varies and some incomplete tabulae have been observed ('tube narrowings'). Wall structure is elongate spherulitic. Spicules have not been found.

MEASUREMENTS (in mm)		S10469
calicle diameter:	mean	0·20
	S.D.	0·046
	range	0·10–0·27
	N	20
wall thickness		0·04–0·09

REMARKS. The measurements of the Klipstein specimen correspond comparatively well with *'Seelandia' lagaaiji* Bizzarini & Braga, 1978 but the external growth-form with the well-developed epitheca is different. However, the potential range of variation in growth-form is not known in this species.

The measurements of *Atrochaetetes 'medius'* given in Dieci *et al.* (1977) do not correspond with the measurements of *Atrochaetetes medius* mentioned in Cuif & Fischer (1974), but match well with the measurements of *Atrochaetetes lagaaiji* (Bizzarini & Braga, 1978).

2. *Cassianopora* Bizzarini & Braga, 1978

[= *Tubuloparietes* Schnorf, 1960.]

Cassianopora Bizzarini & Braga, 1978 is identical with the 'hydrozoan' genus *Tubuloparietes* Schnorf, 1960. Both show slightly irregular calicles with tabulae and the same granular-vacuolar microstructure of the skeleton. The systematic position of the genus *Tubuloparietes*, however, is unclear. Schnorf (1960) placed it within the family Milleporidiidae of the Hydrozoa. Since a great many putative fossil Hydrozoa are calcified demosponges, this too might be a sponge, though the granular-vacuolar wall structure is not yet known from any genuine calcified demosponge.

3. *Zlambachella* Flügel, 1961

From the Austrian Rhaetian, Flügel (1961) described *Zlambachella alpina* as the only species of a new monotypic genus of trepostome bryozoans. Schäfer & Fois (1987) questioned the bryozoan affinities of this species, and inspection of Flügel's figures suggest that this *Z. alpina* may be a calcified demosponge. Growth-form resembles that of the Triassic calcified demosponges described above, boundaries of the tube walls are diffuse, walls do not appear to thicken distally, and the putative acanthostyles are dissimilar from most bryozoan acanthostyles and may be borings.

Bryozoan specimen in the Klipstein Collection

Phylum **BRYOZOA** Ehrenberg, 1831
Class **STENOLAEMATA** Borg, 1926
Order **TREPOSTOMATA** Ulrich, 1882
Suborder **AMPLEXOPOROIDEA** Astrova, 1965
Family **DYSCRITELLIDAE** Duneava & Morozova, 1967

Genus ***DYSCRITELLA*** Girty, 1911

Dyscritella zardinii Schäfer & Fois, 1987 Fig. 9

1984 *Arcticopora* sp.; Boardman: 22; figs 4A–C.
1987 *Dyscritella zardinii* Schäfer & Fois: 179; pl. 2, figs 1–5.

MATERIAL. BMNH D54220 (specimen and oblique longitudinal and transverse acetate peels), Klipstein Colln. Fig. 9A–D.

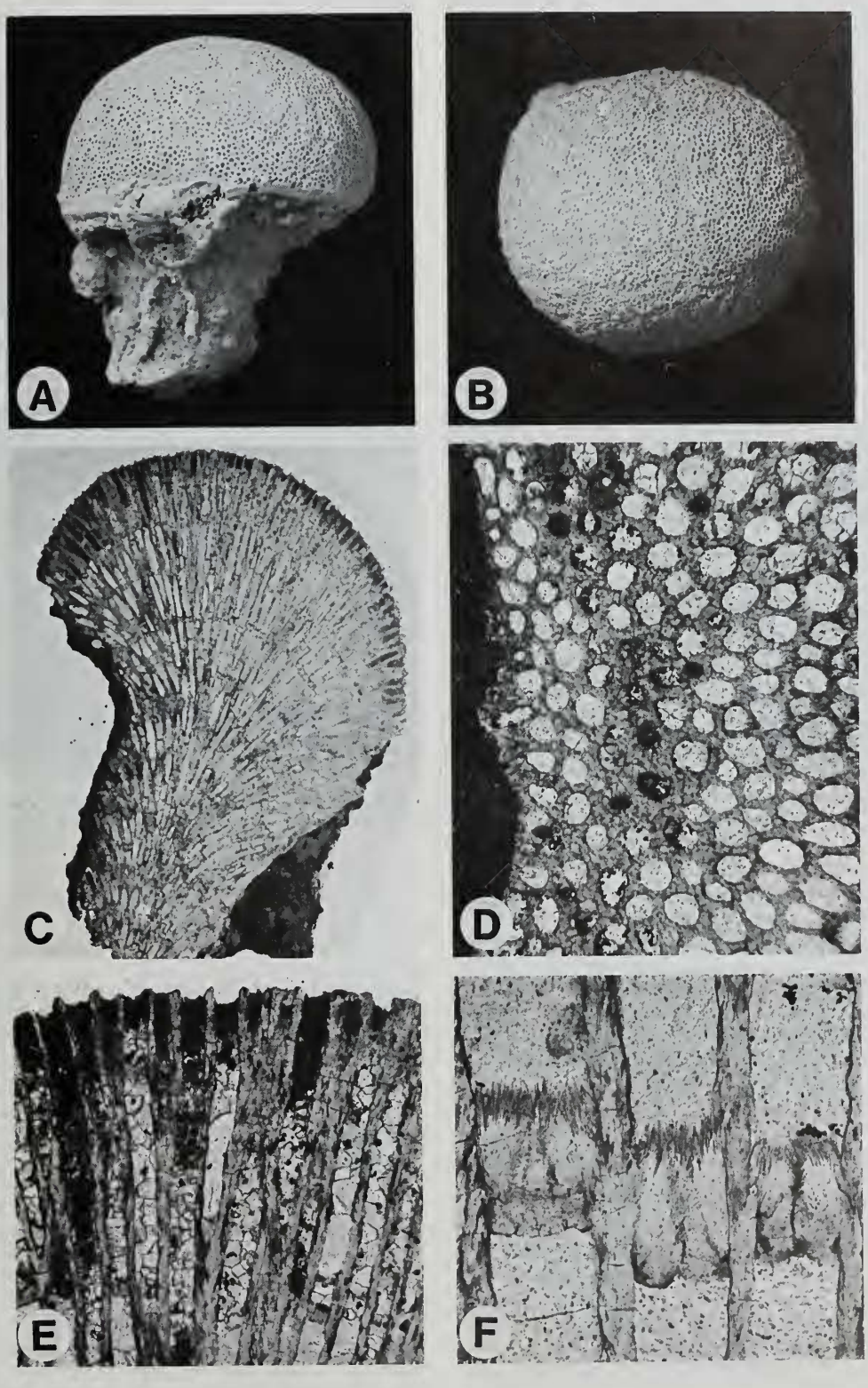

Fig. 8 *Atrochaetetes lagaaiji* (Bizzarini & Braga). Cassian Fm., St Cassian. S10469. A, side view, × 3·3. B, top view showing astrorhizae, × 3·3. C, longitudinal section showing bands of tabulae, × 4·9. D, transverse sections of calicles and epitheca (left), × 21. E, longitudinal section of calicles, × 21. F, tabulae with straight lower edges, × 89.

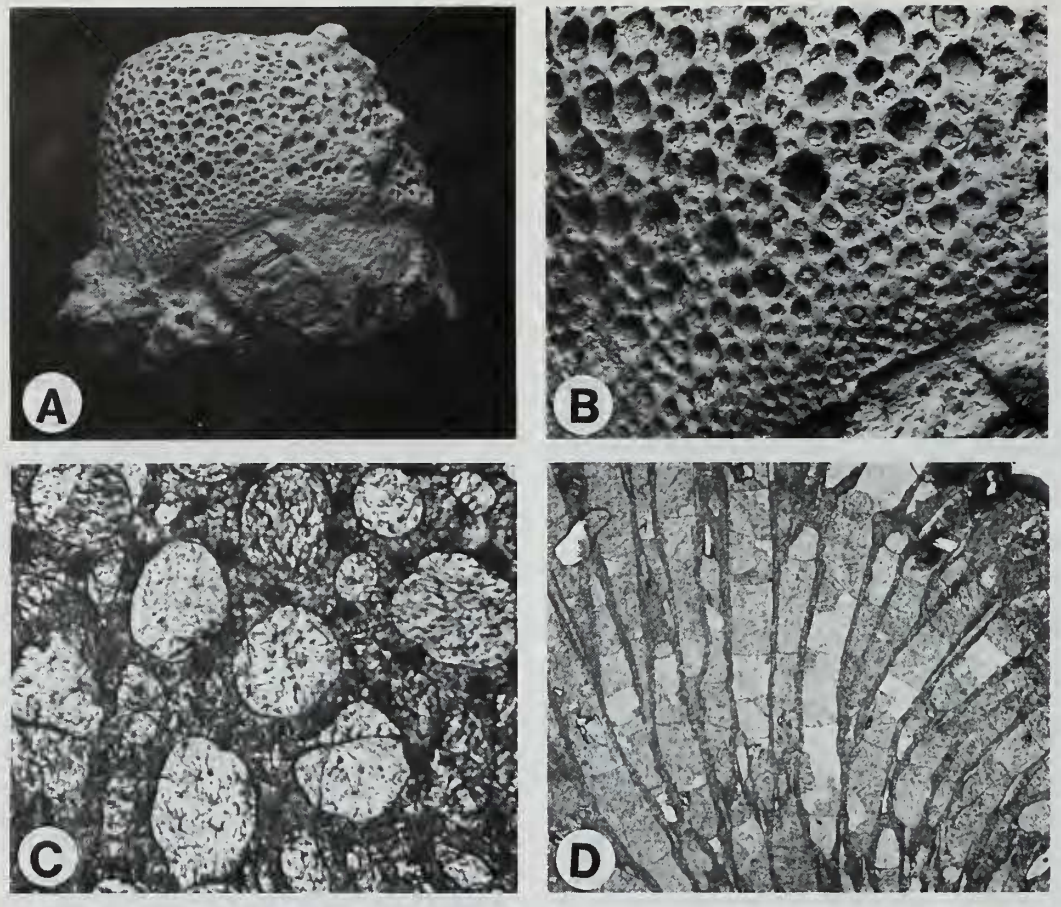

Fig. 9 *Dyscritella zardinii* Schäfer & Fois. Cassian Fm., St Cassian. D54220. A, scanning electron micrograph of colony, × 13. B, micrograph of growing edge, × 41. C, tangential acetate peel showing autozooecia, exilazooecia and styles, × 89. D, oblique longitudinal peel of zooecia, × 31.

LOCALITY AND HORIZON. St Cassian, Italy; Cassian Formation, lowermost Carnian.

DESCRIPTION. A high dome-shaped colony, small (*c.* 4 mm in diameter), with rounded autozooecial apertures, very occasionally petaloid, arranged semi-regularly over the upper surface of the colony and interspersed with and typically surrounded by smaller, variably-sized apertures of exilazooecia. At the edge of the colony close to the basal lamina are immature zooecial buds with very small apertures. Maculae cannot be distinguished.

In section, differentiation between endozone and exozone is poor; zooecial walls are of about the same thickness (0·03 mm) in the endozone as the exozone. Zooecia curve gently towards the colony surface. Exozonal walls in longitudinal section show rounded laminations. Styles with clear cores are abundant, originating in the endozone and continuing into the exozone, and sometimes having a diameter very slightly greater than endozonal zooecial wall width, in which case they indent zooecial chambers. They are of one size only, and about 6–8 styles surround each zooecium in the endozone. Thin-walled basal diaphragms are fairly numerous in the autozooecia, spaced semi-regularly at distances between 0·18 and 0·28 mm, and are flat or slightly concave orally.

MEASUREMENTS (in mm, from the colony surface)	D54220
autozooecial apertural diameter	0·14–0·18, mean 0·16
exilazooecial apertural diameter	0·05–0·11, mean 0·08

REMARKS. The Klipstein Collection specimen differs only in detail from the original description of this Cassian Formation species by Schäfer & Fois (1987).

DISCUSSION

With the exception of one specimen, all of the supposed bryozoans in the Klipstein Collection, including figured type specimens of Klipstein's new species, are sponges and not bryozoans. This confirms the opinion of Boardman (1984: 24) that many Alpine Triassic fossils originally described as bryozoans (see Flügel 1963) belong to other groups. Whereas most of these questionable or non-bryozoans have been previously regarded as cerioporine cyclostomes, there are many records of undisputed Triassic bryozoans assigned to the trepostomes (Bizzarini & Braga 1982; Boardman 1984; Hu 1984; Morozova & Zharnikova 1984; Sakagami 1985; Morozova 1986; Schäfer & Fois-Erickson 1986; Schäfer &

Fois 1987), and some cystoporates, cryptostomes (Schäfer & Fois 1987) and tubuloporine cyclostomes (Bizzarini & Braga 1985 and references therein).

Difficulties in distinguishing between Triassic sponges and bryozoans are a consequence of similarities in overall colony-form, and the size and arrangement of the calicles/zooecia. However, the following morphological criteria can be used when deciding the affinities of problematical Triassic fossils:

1. Skeletal composition. All calcified bryozoans older than late Cretaceous, and all known stenolaemate bryozoans, have calcitic skeletons. Although aragonitic skeletons occur in some species of cheilostomatous gymnolaemates (see Poluzzi & Sartori 1975), cheilostomes usually have box-like zooecia which are quite unlike the long tubular zooecia found in the questionable bryozoans from the Triassic, and make their first appearance in the latest Jurassic. Calcified demosponges can have calcitic or aragonitic skeletons. Therefore, an aragonitic composition strongly suggests a sponge affinity.

2. Skeletal microstructure. Stenolaemate bryozoans generally have walls with a lamellar microstructure, sometimes divided into several distinct units. The laminae usually parallel growth surfaces but can be perpendicular (Boardman *in* Boardman *et al.* 1983). Walls between zooecia (interzooecial walls which constitute the bulk of the skeleton in cerioporine cyclostomes and in trepostomes) are often bilaterally symmetrical and may have a median granular layer (see Tavener-Smith & Williams 1972). In contrast, the walls of calcified demosponges have fibrous microstructures, the fibres arranged either in spherules or in radiating fans (cligonal or water-jet structure), or alternatively, lamellar microstructures. There is no clear median division of the wall. The finding of a fibrous microstructure in a Triassic fossil of questionable affinities permits its identification as a sponge.

3. Spicules. Although cheilostome bryozoans belonging to the Family Thalamoporellidae have calcareous spicules in their zooids (Soule & Soule 1970), spicules are not known to occur in stenolaemates or any pre-Cenozoic bryozoans. Some species of calcified demosponges incorporate originally siliceous spicules into the calcareous walls of the calicles (e.g. Fig. 3F). Therefore, the occurrence of spicules in a Triassic fossil is a reliable indicator of a sponge affinity.

4. Styles. Many Palaeozoic stenolaemate bryozoans contain within their walls skeletal rods termed styles (= acanthopores or acanthostyles). Styles have a cone-in-cone microstructure, often with a non-laminated core, may project as spines at the colony surface and indent the outlines of the zooecial apertures (see Boardman *in* Boardman *et al.* 1983). There are no equivalent structures in calcified demosponges.

5. Budding. Patterns of zooecial budding in stenolaemate bryozoans vary (McKinney 1975, 1977), but new buds always arise by the splitting of a zooecial wall such that there is no confluence between the chambers of the parent and daughter zooecia. Although a similar form of budding may be observed in calcified demosponges, where it is known as intraparietal budding, fissipar budding in which the calicles are confluent may also occur.

6. Wall-chamber boundaries. These boundaries are invariably sharp in stenolaemate bryozoans, whereas they are often ragged and indistinct in calcified demosponges.

7. Diaphragms/tabulae. Stenolaemate zooecia are often partitioned horizontally by diaphragms (see Boardman *in* Boardman *et al.* 1983) secreted by epithelial tissue situated on their oral or aboral sides. They have a lamellar microstructure, are typically thin-walled and of an even thickness, and in cerioporine cyclostomes may be penetrated by pseudopores. Tabulae, the equivalent structures in calcified demosponges, often differ from diaphragms in being thick-walled and varying considerably in thickness across the calicle.

8. Backfilling. Some calcified demosponges partially or completely fill the old parts of their calicles with calcification. Stenolaemate bryozoans are not known to do likewise.

9. Endozone–exozone differentiation. Colonies of stenolaemate bryozoans, notably trepostomes and cerioporine cyclostomes with arborescent branching growth-forms, are frequently divisible into an axial endozone surrounded by an exozone. The endozone contains the proximal parts of the zooecia which tend to be thin-walled and orientated parallel to the growth direction of the branch. Budding of new zooecia may be concentrated in or confined to the endozone. Passing from the endozone into the exozone, the zooecia bend abruptly until their long axes are typically subperpendicular to branch growth direction. The walls of the zooecia in the exozone are usually relatively thick, and various morphological characters (e.g. diaphragms, styles) may be present in only one zone or may change in frequency between zones. Such endozone–exozone differentiation, although not developed in all stenolaemates, has no equivalent among calcified demosponges.

10. Monilae. Some trepostomes and cerioporine cyclostomes have annularly thickened zooecial walls which are described as moniliform (see Boardman 1984). These thickenings can be very regular, and are unlike any structures described in calcified demosponges.

11. Pores. Cerioporine cyclostomes are characterized by the presence of small pores in the zooecial walls; trepostomes always lack such pores. Pores are often distributed in the thin-walled parts of the walls between moniliform thickenings and many thin sections fail to intersect them. Small regular pores are generally absent in calcified demosponges which may, however, possess large, irregular gaps in the walls of the calicles.

12. Zooecium/calicle diameter. One of the reasons for the persistent confusion between calcified demosponges and bryozoans is undoubtedly the similarity in diameter of the tubes in the two groups. However, the largest calicles in calcified demosponges exceed the range of variation known for stenolaemate bryozoans. Zooecial diameter in most trepostomes is between 0·1 and 0·3 mm, with a maximum value of 0·46 mm (Anstey & Perry 1972). Calicle diameter in living and fossil calcified demosponges ranges from about 0·12 to *c.* 1·2 mm, although the maximum size in living species is about 0·6 mm (Scrutton 1987). Therefore, any problematical fossil with a tube diameter in excess of 0·5 mm must be suspected to be a calcified demosponge.

13. Early growth stages. The first-formed zooid–the ancestrula–in a stenolaemate bryozoan colony is distinctive in possessing a hemispherical proximal part, termed the protoecium, out of which there emerges a distal ancestrular tube (e.g. Podell & Anstey 1979). Although the ancestrula is normally overgrown by later zooecia, sections cut at the base of the colony may reveal the presence of an ancestrula and permit inference of bryozoan affinity.

14. Astrorhizae. Some calcified demosponges have on their surface a system of shallow, radiating grooves–astrorhizae–which reflect the distribution of exhalant canals in the living sponge. The only bryozoan structures likely to be confused with astrorhizae are the stellate maculae found in the

cystoporate family Constellariidae (see Utgaard *in* Boardman *et al.* 1983). However, the radial structure in stellate maculae is formed by rays composed of zooecia and inter-rays of vesicles. Furthermore, constellariids range no higher than the Lower Silurian.

15. Brood chambers. Spacious skeletal chambers are present in cerioporine cyclostomes for the brooding of larvae. Brood chambers have pseudoporous roofs which are typically supported by occasional zooecia and septa that penetrate the chamber; they are normally easy to recognize in thin section (e.g. Nye 1976: pl. 32, figs 1e–f). Both trepostome bryozoans and calcified demosponges are lacking structures of this morphology.

For both calcified demosponges and bryozoans, the Triassic represents a critical time in their evolutionary history. The phylogenetic relationships between Palaeozoic and post-Palaeozoic representatives in each group are poorly understood. Clarification of these problems must include a re-evaluation of supposed fossil sponges and bryozoans from the Triassic to ascertain their true taxonomic affinities.

Study of a small number of specimens in the Klipstein Collection from St Cassian has revealed the existence of eight different calcified demosponge species. There is a clear need for further studies to obtain a more accurate estimate of the full diversity of the rich St Cassian sponge fauna, and to provide more complete descriptions of the sponge species and their variability.

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